

THE LAYING OF REPLACEMENT CLUTCHES BY FALCONIFORMS AND STRIGIFORMS IN NORTH AMERICA

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Abstract

This paper discusses the laying of replacement clutches by North American raptors by reviewing existing literature and presenting data gathered from oological collections and from the double-clutching of wild and captive birds. We found that most species recycle; however, the frequency of recycling declined with an increasing stage of incubation. Clutch size did not decrease significantly between layings for most species. Although a single replacement clutch was usually laid, multiple replacements are known. After loss of the first clutch, raptors usually renested in the same site. If a new location was used, it was usually in close proximity to the original site. Although data from areas north of southern Canada were scarce, it appeared that recycling was rare in arctic regions. We concluded that double-clutching can be used in most management plans for North American raptors.

Introduction

That certain birds of prey possess the ability to lay an additional set of eggs after loss of their initial clutch has long been known (e.g., Wade 1882; Barlow 1897). Most early data on the laying of these replacement clutches were gathered by oologists who noted this occurrence after removing clutches (Bent 1937, 1938; Newton 1977). Replacement clutches have also been mentioned in more recent writings (Beebe 1974; Fyfe 1976; Newton 1977, 1979; Walton 1977). Replacement clutches, resulting from the practice of double-clutching, are now an important part of many propagation projects concerning raptors (Lejeune 1972; Fyfe 1976; Burnham et al. 1978). For double-clutching to be successful, however, data must be available on the response of the species to egg removal. Except for the Peregrine Falcon (*Falco peregrinus*), published data are scarce.

The purposes of this paper are to (1) summarize data in the literature on replacement laying and (2) present new information on this process gathered from oological collections and from the double-clutching of wild and captive birds. The scope of this paper is limited to data concerning mostly North American species. We hope this paper stimulates future work in the area of double-clutching in raptor management and encourages captive breeders to publish data they likely possess concerning replacement laying.

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Table 1. Summary of Data Concerning Various Aspects of Clutch Replacement by North American Raptors Based on Museum Records and Literature References (clutch size based on museum records only).

Species	Recycling time X (N) Range	No. known relays	Clutch size (X;SD)			Incubation stage	Nest sites	Dates (locations)	Sources and relevant literature
			First	ment	N %change				
Barn Owl (<i>Tyto alba</i>)	20 (1) -	1	5.0	4.0	1 nc	Fresh	Same	Apr-May (CA)	1
Long-eared Owl (<i>Nyctio stus</i>)	18 (3) 12-22	1	6.0	6.0	1 nc	10%	Same	Mar-May (CA, OR)	1,24
Short-eared Owl (<i>A. flammea</i>)	- - -	3	7-8	7-8	- nc	-	Same	June (WA)	1
Screech Owl (<i>Otus asio</i>)	22 (2) 14-29	1	3.0	3.5	2 nc	Slight	Same	Apr-May (CA, OR)	1,24
Great Horned Owl (<i>Bubo virginianus</i>)	20 (12) 8-35	1	3.1 (0.94)	2.8 (0.98)	11 -9.7	to 14 days	Same- 100m	Feb-Apr (TX, IA, AZ, CA, WV)	1,24,33
California Condor (<i>Gymnogyps californianus</i>)	37 (2) 33-41	1	1.0	1.0	2 nc	-	Captive	Apr (CA)	18
Black Vulture (<i>Coragyps atratus</i>)	26 (4) 25-27	2	2.0	2.0	4 nc	to 7 days	Same	Jan-Mar (FL)	1
Caracara (<i>Polyborus plancus</i>)	- - -	2	-	-	-	-	-	-	5
Osprey (<i>Pandion haliaetus</i>)	26 (3) 25-28	1	3.5	3.0	2 nc	Fresh	Same	Mar-June (NY, CA)	1,2,4,16,30
Mississippi Kite (<i>Ictinia mississippiensis</i>)	14 (1) -	1	-	-	-	-	Same	-	1,4
White-tailed Kite (<i>Elanus leucurus</i>)	- - 19-22	1	3.0	4.0	1 nc	-	New	Apr (CA)	1,3
Marsh Hawk (<i>Circus cyaneus</i>)	- (1) -	1	4.6	-	-	-	-	Apr-May (MI)	35
Bald Eagle (<i>Haliaeetus leucocephalus</i>)	38 (4) 27-60	1	3.0	2.0	1 nc	Advanced	Same	Dec-Feb (FL)	1,4,13
Goshawk (<i>Accipiter gentilis</i>)	18 (1) -	1	-	-	-	-	-	-	26
Cooper's Hawk (<i>A. cooperi</i>)	13 (2) 10-14d	1	5.0	5.0	1 nc	-	Same to "nearby"	May (CA)	4

		-	-	-	2	-	-	-	-	-	100 m	101, PA, CI
Black Hawk (<i>Buteo calurus anthracinus</i>)											New	28
Harris' Hawk (<i>Parabuteo unicinctus</i>)	23 (1)	-	2	3.0	3.0	1	nc	Started	"Nearby"	Mar-Apr (AZ)	1, 34	
Red-shouldered Hawk (<i>Buteo lineatus</i>)	24 (6)	19-30	1	2.7	2.0	3	nc	to 14 days	Same to "nearby"	Mar-Apr (CA, MI) Jan-Mar (FL)	1, 4, 36	
Broad-winged Hawk (<i>B. platypterus</i>)	13 (4)	12-13	2	2.7	2.0	4	nc	to 7 days	Same to 200 m	May-June (CT)	1, 7	
Swainson's Hawk (<i>B. swainsoni</i>)	27 (2)	24-29	2 ?	3.0	3.0	1	nc	Heavy	Same to 200 m	Apr-July (TX)	1, 22, 25	
White-tailed Hawk (<i>B. albicaudatus</i>)	13 (2)	10-15	1	2.0	2.0	2	nc	Fresh	Same to "nearby"	Mar-Apr (TX)	1, 21	
Red-tailed Hawk (<i>B. jamaicensis</i>)	17 (9)	12-25	1	2.8 (0.67)	2.1* (0.60)	9	-25.0	Slight	Same to "nearby"	Mar-May (PA, OR, CA, TX)	1, 4	
Golden Eagle (<i>Aquila chrysaetos</i>)	24 (10)	19-30	1	2.0 (0.00)	2.2 (0.42)	10	+10.0	One-half	Same	Feb-Apr (CA)	1, 4, 27	
American Kestrel (<i>Falco sparverius</i>)	17 (17)	9-34	3	4.6 (0.92)	4.7 (0.47)	11	+ 2.2	Advanced	Same	Mar-May (CA)	1, 23	
Merlin (<i>F. columbarius</i>)	12 (1)	-	1	5.5	5.5	2	nc	Fresh	"Nearby" to 300 m and NFLd., Can.)	May-June (Albt. 1, 5)		
Prairie Falcon (<i>F. mexicanus</i>)	16 (12)	13-25	1	4.9 (0.33)	4.4* (0.53)	9a, b	-10.2	14, 16, 18, 32 days	Same	Apr-May (CA)	1, 5, 9, 29	
Peregrine Falcon (<i>F. peregrinus</i>)	18 (8)	14-21	2	3.6 (0.55)	3.5 (1.00)	8a	-2.8	to 18 days	Same to 100 m	Apr-June (CA)	1, 5, 6, 8, 10, 11, 12, 14, 15, 17, 19, 20, 32	

* $P < 0.05$, t-test.

a Includes double-clutching experiments by B. Walton.

b Includes four clutches from captive birds.

Cnc=not calculated.

d Includes wild pair observed by B. Walton in 1975.

Reference codes: 1-MVZ, 2-Ames (1966), 3-Barlow (1987), 4-Bent (1937), 5-Bent (1938), 6-Bond (1946), 7-Burns (1911), 8-Cade and Pye (1970), 9-Bawson (1913), 10-Pye (1976), 11-Green (1916), 12-Herbert and Herbert (1965), 13-Herrick (1934), 14-Hickey (1942), 15-Hickey and Anderson (1965), 16-Kennedy (1977), 17-Keyes (1966), 18-Koford (1953), 19-Lejeune (1972), 20-Nethersole-Thompson (1931), 21-Nyc (1941), 22-Olendorff (1975), 23-Porter and Wiemeyer (1972), 24-Sclater (1912), 25-Sharp (1902), 26-Simpson (1909), 27-Slevin (1929), 28-Thomas (1908), 29-Tyler (1923), 30-Tyrell (1956), 31-Wade (1882), 32-Walton (1977), 33-Wolfe (1912), 34-Wader (1977), 35-Craighead and Craighead (1956).

Methods

The data accompanying egg sets housed at the Western Foundation of Vertebrate Zoology (WVZ) were studied; data transcribed included date and location of collection, clutch size, incubation stage, nest site, collector, and collector's comments. Because incubation terminology has not been standardized, date of set collection was corrected on the basis of reported incubation to give date of clutch initiation. Using the approximate incubation period of a species (Bent 1937, 1938; Brown and Amadon 1968; Newton 1977), the date of clutch initiation was estimated by subtracting stage of incubation in days from date of set collection (Anderson and Hickey 1970; L. F. Kiff, ms). Data gathered by Walton while experimenting with double-clutching wild and captive Peregrine and Prairie (*F. mexicanus*) Falcons are also presented.

To help standardize terminology, the following definitions were applied to several important terms: replacement clutch—the set of eggs laid following loss (natural or artificial) of a previous set (can apply to more than one replacement); double-clutching—the practice of removing a set of eggs with the purpose of initiating the laying of an additional clutch (i.e., the replacement clutch); recycling—the act of laying an additional set of eggs after loss of a previous set. The terms *set* of eggs and *clutch* are synonymous.

Results and Discussion

A summary of data (table 1) reveals the scattered nature of available information on recycling. It was evident, however, that most North American falconiforms and strigiforms recycled even when incubation was in an advanced stage; however, the frequency of recycling apparently decreased with an increasing stage of incubation (see also Green 1916; Hickey 1942; Craighead and Craighead 1956; Newton 1977). The upper limit on recycling appeared to be after about 25 days incubation, although recycling did occur after longer periods (table 1). In falcons, the frequency of recycling was highest if eggs were removed after 7 to 10 days of incubation (Fyfe 1976). No clear trends were shown when we correlated stage of incubation when eggs were lost with recycling time; this was not surprising given our relatively small sample sizes. It is likely that species-specific behavioral, physiological, and environmental controls of breeding are likely important in setting limits on recycling.

It appeared that clutch size decreased slightly with subsequent layings for most species. In those species with a relatively large sample size, only the Red-tailed Hawk (*Buteo jamaicensis*) and Prairie Falcon showed a significant decrease in clutch size between layings (table 1). In no case did clutch size decrease the equivalent of one egg. This should thus be considered a weak trend that varies among individuals of a species. While experimenting with double-clutching the Osprey (*Pandion haliaetus*), Kennedy (1977) found clutch size to be smaller (3.0 vs. 2.6 eggs) for the second clutch; however, hatching rate of second clutches exceeded that of single-clutched birds.

In reviewing recycling in various birds, Lack (1954) concluded that physiological exhaustion of the female was not responsible for a reduction in clutch size. He felt that other factors, especially reduced food availability as the season progressed, likely influenced the size of the replacement clutches. Prey abundance should thus be analyzed concomitantly with studies of double-clutching in raptors.

Most records (WVZ data and literature sources) recounted the laying of a single replacement clutch; several cases of multiple replacements are known. In New York, Herbert and Herbert (1965) noted the laying of four clutches within a two-month period by a Peregrine Falcon. A captive American Kestrel (*F. sparverius*) laid five clutches within

a 61-day period; the first four clutches each contained five eggs, and the fifth clutch decreased to three eggs (Porter and Wiemeyer 1972). By removing each egg as it was laid, Wade (1882) was able to induce several Sharp-shinned Hawk (*Accipiter striatus*) to lay 15 to 18 eggs during a one-month period. It is evident that many raptors possess the potential to lay more than one replacement clutch in a season.

Loss of eggs usually did not cause a shift in nest site (table 1). If a new nest was constructed, it was usually within several hundred meters of the original site. Although we cannot know the exact effects that clutch removal has on the behavior of raptors, the lack of any overt response implies that only minor harm results; egg removal by man likely simulates natural egg loss. The role that time of season of egg removal has on nest site selection and breeding success needs study.

Hickey (1942) and Beebe (1974) stated that recycling does not occur at "high latitudes." However, data presented herein on the Merlin (*F. columbarius*) showed recycling to take place in Newfoundland. Peregrine Falcons are known to recycle in Alberta (Cade and Fyfe 1970) and in the Queen Charlottes (Cade 1960), Canada, whereas in the arctic re-nesting is not likely to be successful (Cade 1960). The Bald Eagle (*Haliaeetus leucocephalus*) nesting in Alaska did not recycle after loss of eggs (Hensel and Troyer 1964). This was also true for eagles in the Aleutians (52° N. Lat.) when eggs were lost only 5 days after clutch completion (C. M. White, pers. comm.). The frequency of recycling apparently declines north of the southern tier of Canadian provinces. Studies such as those of Cade (1960), in which the onset and duration of the breeding cycle can be related to latitude, are needed prior to initiation of any raptor management plan that involves recycling.

Newton (1977) stated that recycling was relatively infrequent among buzzards and kites, and rare among eagles. Beebe (1974) felt that Bald Eagles would not recycle in the same season. Although results of this study show that these species do recycle, the relative frequency of recycling must remain speculative until additional data are collected. However, there is the possibility that double-clutching can be used as a method of increasing productivity in both species of North American eagles.

Except for Prairie and Peregrine Falcons, information presently available does not allow a description of the optimal stage of incubation or breeding season to initiate recycling. Data do show that double-clutching can be employed in most, if not all, management plans concerning North American falconiforms and strigiforms.

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PROBABLE PREDATION ON WHITE-TAILED KITE BY RED-TAILED HAWK

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Though Red-tailed Hawks (*Buteo jamaicensis*) may prey upon a variety of both vertebrate and invertebrate animals (Sherrod 1978), reports of their predation on raptors are apparently rare. Drawing from a handful of observations, classical summaries of the Red-tailed Hawk's diet include Red-tailed Hawk, Red-shouldered Hawk (*Buteo lineatus*), and Screech Owl (*Otus asio*) as known prey (Bent 1937; Fitch et. al. 1946). More recently, cannibalism involving adult Red-tailed Hawks was reported by Clevenger and Roest (1974).

On 2 January 1978, the freshly killed carcass of a White-tailed Kite (*Elanus leucurus*) was found on the ground at the entrance of Armand Bayou Nature Center in southeast Harris County, Texas, in a spot from which a large Red-tailed Hawk had flown only moments before. The head had been completely removed and apparently eaten; only the lower mandible and a single quadrate bone remained. The furcular area had been cleared of tissue through the breast muscles to the sternum. Many dorsal feathers had been removed and lay scattered around the carcass. The otherwise intact carcass was salvaged and placed in the Texas Cooperative Wildlife Collections at Texas A&M University, College Station (TCWC, No. 10418). The kite was an adult female.

We did not see the actual kill but assume that it was predation and not scavenging for the following reasons. First of all, it seems unlikely that the hawk discovered a kite